

Sexual Dimorphism in Stature and Women's Work: A Phylogenetic Cross-Cultural Analysis

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ABSTRACT The following cultural variables were tested for their association with sexual dimorphism: sexual division of labor, type of subsistence (hunting and agriculture), and polygyny. The transmission of these traits among populations was investigated. All the traits were found to be associated with phylogeny, indicating that they are inherited from mother to daughter populations. A cross-cultural comparative method was used which controls for the statistical effects of similarity due to common ancestry (Galton's problem). Cross-cultural variation in sexual dimorphism in stature is negatively associated with women's contribution to subsistence. Women are taller, relative to men, in societies where women contribute more to food production. This may be because female nutritional status is better in these societies. No relationship was found between sexual dimorphism and other aspects of subsistence or polygyny. These results are discussed in relation to other studies of sexual dimorphism in modern and archaeological populations, and in relation to cross-cultural variation in sex-biased parental investment. *Am J Phys Anthropol* 110:27–45, 1999. © 1999 Wiley-Liss, Inc.

In all populations, mean male stature is greater than mean female stature, but there is variation in the degree of sexual dimorphism among populations. Here we investigate the correlates of interpopulation variation in sexual dimorphism in a worldwide sample of 76 nonindustrial populations. The aim was to test two hypotheses for cross-cultural variance in sexual dimorphism in stature, while controlling statistically for the effects of relatedness among populations (Galton's problem).

The first hypothesis to be tested is that sexual dimorphism in stature is associated with mating and marriage, and is greater in populations with polygynous marriage because intramale competition for females is higher in these populations (Trivers, 1972; Alexander et al., 1979). The second hypothesis is that sexual dimorphism is associated

with variation in the sexual division of labor, where natural selection for subsistence activities is different for the two sexes (Frayser, 1980; Brace and Ryan, 1980). Both theories descend from Darwin (1874), who suggested that sexual dimorphism can evolve through sexual selection, and as a result of different natural selection pressures on males and females in species where the two sexes occupy different ecological niches. These hypotheses were first proposed to explain variance in sexual dimorphism across species, but may also explain part of the cross-cultural variance in sexual dimorphism in stature in humans.

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HISTORICAL RELATEDNESS AMONG CULTURES

Human cultures are hierarchically related by descent, and therefore are not independent for the purposes of statistical analysis. This is known as Galton's problem, first recognized by Francis Galton in 1889 (Tylor, 1889). Ancestrally related populations share multiple traits (cultural and genetic) which they have inherited from their common ancestors (Guglielmino et al., 1995; Holden and Mace, 1997). Related populations are also similar because daughter populations tend to inhabit similar environments (Harvey and Pagel, 1991; Mace and Pagel, 1994, 1997; Mace and Holden, 1999). Treating cross-cultural data as if they were independent is liable to produce spurious statistical associations between functionally unrelated characters which have simply been inherited together from a common ancestor. It can also obscure real relationships among variables against a background of ancestral dissimilarity (Harvey and Pagel, 1991).

Horizontal and vertical transmission of biocultural traits

Genetic and cultural traits can be transmitted between neighboring populations (horizontal transmission) as well as from mother to daughter populations (vertical transmission). The first part of our analysis aimed to investigate whether the variables in the analysis are transmitted vertically or horizontally, or both. If a trait is transmitted from mother to daughter populations, it is necessary to use a statistical method which controls for the effects of similarity due to relatedness among populations when investigating the evolutionary correlates of the trait. A horizontal transmission event, in terms of the phylogenetic model used here, is statistically equivalent to an independent evolutionary event. The phylogenetic model allows one to distinguish between inheritance and *de novo* acquisition of a trait, in order to test for correlated change among traits.

In our investigation of how traits are transmitted among populations, we tested whether each trait studied (e.g., degree of sexual dimorphism, hunting, agriculture, polygyny, and women's work) was associated with a population's closest phylogenetic rela-

tives and/or its nearest geographical neighbors. If a trait is associated with phylogenetic relatives this indicates that it is transmitted vertically, from mother to daughter populations. If a trait is associated with nearest geographical neighbors this indicates that it is transmitted horizontally, between neighboring populations. Phylogenetic relatives were defined as the genetic sister-group of each population on a genetic tree. Nearest geographical neighbors were found using great-circle distances. Multiple regression was used to investigate the association between each trait in the populations in the sample (the dependent variable) and in their phylogenetic relatives and geographical neighbors (the independent variables).

All the traits tested showed a significant association with phylogeny (see below). A phylogenetic comparative method, which controls for similarity due to inheritance among related populations, is therefore necessary when investigating correlations among these traits.

Controlling for Galton's problem in cross-cultural analysis

In anthropology, the most widely used method of controlling for Galton's problem is to exclude closely related populations from the cross-cultural sample. The "Standard Cross-Cultural Sample" of 186 populations worldwide is the most widely used holocultural sample. It was designed as a representative worldwide sample, from which closely related cultures were excluded (Murdock and White, 1969). However, excluding closely related populations from the sample does not eliminate similarities among populations inherited from more distant ancestors. Moreover, it results in the loss of potentially informative variance among closely related populations, thereby increasing the likelihood of Type II errors (failing to detect real patterns in the data). An alternative method of controlling for Galton's problem is used here, a phylogenetic comparative method which was developed in evolutionary biology to control for nonindependence among species which are related by descent.

Phylogenetic comparative analysis tests for correlated evolutionary change in two characters, or in a character and an environ-

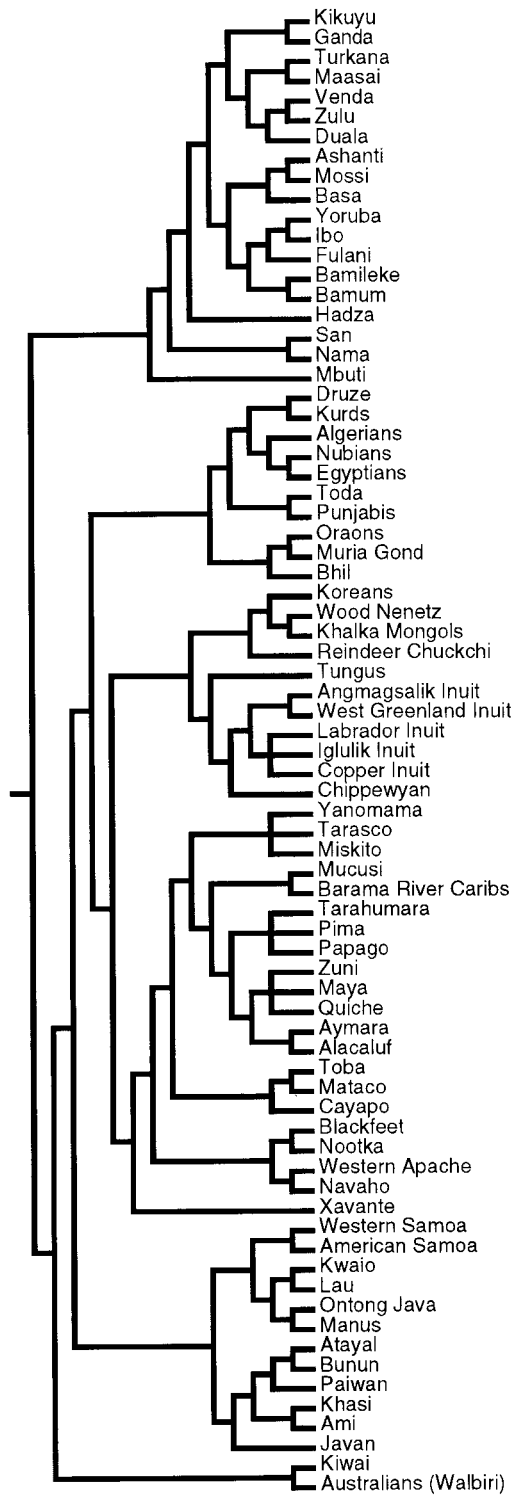


Fig. 1. Genetic tree adapted from Cavalli-Sforza et al. (1994), used in the comparative analysis using independent contrasts.

mental variable. First, a model of the historical relationships among populations (a phylogeny) is constructed, based on either genetic or linguistic similarity. There is considerable evidence that language trees provide information about population history, because both genetic and linguistic divergence follow from isolation by distance, or from cultural or geographical barriers among populations (Cavalli-Sforza et al., 1988; Barbujani, 1991; Penny et al., 1993). Character states at internal nodes of the tree (i.e., ancestral character states) are estimated from character states at the tips of the tree (i.e., in extant populations, from a cross-cultural sample). Instances of evolutionary change in characters along the branches of the tree are counted as "independent contrasts." Character change along any branch of the tree is independent of character change in any other branch, thereby avoiding the problem of statistical nonindependence due to relatedness of populations. In this method, evolutionary changes in characters in the past (called independent contrasts) are counted as independent observations for statistical analysis, rather than character states in the cross-cultural sample (Felsenstein, 1985; Pagel, 1992; Mace and Pagel, 1994, 1997).

HYPOTHESES FOR CROSS-CULTURAL VARIATION IN SEXUAL DIMORPHISM

Polygyny

The first hypothesis to be tested is that sexual dimorphism is associated with polygyny. This hypothesis stems from Darwin (1874), who suggested that many aspects of sexual dimorphism, including size dimorphism, are sexually selected through competition among males for females in polygynous species. Across many mammalian groups, including pinnipeds, ungulates, and nonhuman primates, size dimorphism has been associated with polygyny (Alexander et al., 1979; Leutenegger, 1982; Andersson, 1994). Trivers (1972) hypothesized that cross-cultural variance in sexual dimorphism among humans may be associated with cross-cultural variation in mating or marriage patterns. A number of studies have tested this hypothesis.

Alexander et al. (1979) tested the hypothesis that sexual dimorphism in stature is

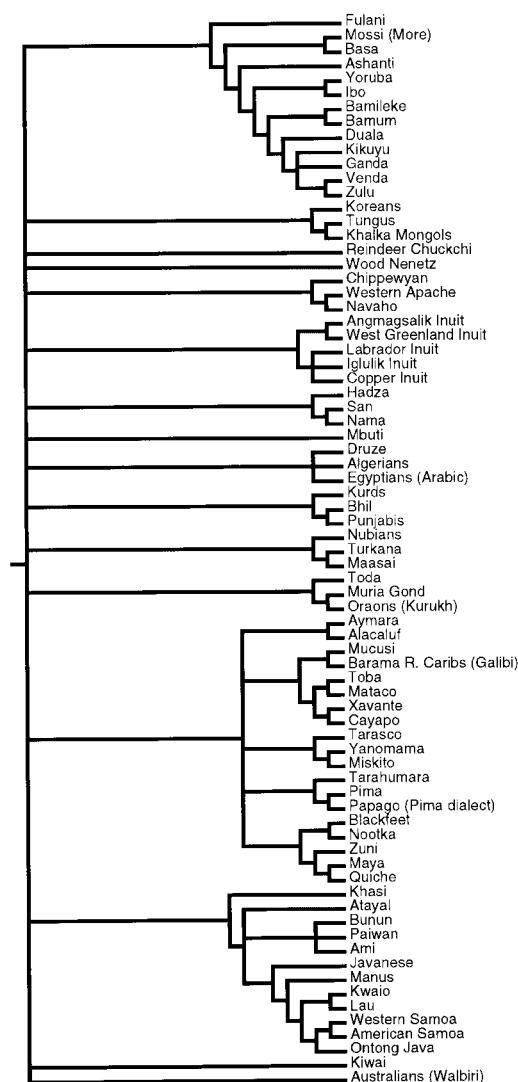


Fig. 2. Language tree adapted from Ruhlen (1991), assuming a single origin of languages, used in the comparative analysis using independent contrasts.

greater in polygynous societies than in monogamous societies in a cross-cultural sample of 93 human populations. In their initial analysis, they found no difference in sexual dimorphism in stature between the 47 monogamous and 46 polygynous societies in the sample. They then divided the monogamous societies into two groups: "ecologically" and "socially" imposed monogamy. Ecologically imposed monogamy is found in marginal habitats, e.g., among some hunter-

gatherers. The ecological basis of this type of monogamy was argued to be comparable to monogamous mating in other species, i.e., a relatively equal distribution of resources among males (Orians, 1969). Socially imposed monogamy occurs in societies where there is high variance in wealth and resources among males, i.e., where one would expect wealthy males to mate polygynously. Alexander et al. (1979) argued that socially imposed monogamy is a historically recent phenomenon, in which monogamy is imposed by the state. There were 16 societies in the sample with ecologically imposed monogamy, and 31 societies with socially imposed monogamy. The ratio of male to female stature in ecologically imposed monogamous societies was 1.068 cm, compared to 1.078 cm in polygynous and socially imposed monogamous societies.

Gray and Wolfe (1980) criticized the study of Alexander et al. (1979) because it did not use an independent source of information about marriage practices. Subsequent investigations into the relationship between sexual dimorphism in stature and polygyny have used the *Ethnographic Atlas* of Murdock (1967, 1986) as a source of data about marriage across cultures. Gray and Wolfe (1980) and Wolfe and Gray (1982a) found no support for the results of Alexander et al. (1979), using data on marriage and social organization from Murdock (1967). Gaulin and Boster (1992) did replicate the results of Alexander et al. (1979), using data on marriage and social stratification from Murdock (1986). However, the relationship disappeared when they excluded estimates of sexual dimorphism from samples of fewer than 10 individuals of each sex, suggesting that it was an artifact of poorly sampled populations. In summary, most previous studies do not support the hypothesis that cross-cultural variation in dimorphism in stature is associated with polygyny.

Sexual division of labor

The second hypothesis can also be traced back to Darwin (1874), who suggested that sexual dimorphism can evolve through natural selection in species where males and females occupy different ecological niches, e.g., different foraging strategies. A math-

ematical model of the evolution of sexual dimorphism through ecological divergence between the sexes was formulated by Slatkin (1984). Evidence for the ecological niche hypothesis of sexual dimorphism in animals was reviewed by Shine (1989).

Human societies are characterized by marked sexual division of labor in subsistence activities, the equivalent of animal foraging strategies (Murdock and Provost, 1973). Natural selection on traits related to food production might therefore be different in males and females. This hypothesis has been developed in paleoanthropology. Frayer (1980, 1981) and Brace and Ryan (1980) hypothesized that changes in the subsistence activities of males and females may explain the decline in sexual dimorphism since the Late Paleolithic. Large-game hunting was a more important subsistence activity in the Late Paleolithic than in later periods (Frayer, 1981). In contemporary populations, large-game hunting is almost exclusively a male activity (Murdock and Provost, 1973). By ethnographic analogy, it was probably also a male activity in the Late Paleolithic. It is hypothesized that males in the Late Paleolithic were selected for physical strength and size because they hunted large animals using spears (Frayer, 1980, 1981; Brace and Ryan, 1980). Selection for hunting ability in males may also be partly sexual selection, if meat is exchanged for sex with females (i.e., hunting is part of male mating effort). Hill and Hurtando (1996) found that among the Ache, modern hunter-gatherers in South America, there was a highly significant positive relationship between male fertility and hunting skill. Women's subsistence activities in contemporary foraging societies, such as gathering, are less dependent on physical strength (Murdock and Provost, 1973). One would expect females to be under different selection pressures, perhaps for earlier maturation or maximum energy efficiency (Andersson, 1994). It is hypothesized that as a consequence of the different selection pressures on males and females, sexual dimorphism was high in the Late Paleolithic.

In the Mesolithic, there was a shift towards hunting smaller, less dangerous game, and also the invention of the bow and arrow,

which reduced selective pressures on males for large size. Male size decreased, perhaps because a smaller body size requires less energy and protein for maintenance (Frayer, 1980, 1981). Sexual dimorphism was reduced as a consequence. With the advent of agriculture, there was probably a convergence of male and female subsistence activities. In modern agricultural populations, there is more overlap in male and female subsistence activities than in hunter-gatherers (Murdock and Provost, 1973). Selection pressures on stature in males and females therefore also converged, and sexual dimorphism was further reduced.

Archaeological evidence for a reduction in sexual dimorphism over time, coinciding with changes in subsistence, especially the advent of agriculture, varies across regions. Frayer (1980, 1981) found evidence for a decline in sexual dimorphism from the Late Paleolithic through the Mesolithic to the Neolithic in Europe. In contrast, Meiklejohn et al. (1984), using a different sample, found that sexual dimorphism declined in Europe between the Late Paleolithic and the Mesolithic, but increased in the Neolithic. In the Levant, Smith et al. (1984) found no evidence of change in either sexual dimorphism or hunting behavior between the Late Paleolithic and the Neolithic. Kennedy (1984) found that in South Asia the advent of agriculture (from ca. 6500 BP) was associated with a decline in sexual dimorphism and stature, which he related to low protein intake in agricultural populations. In coastal Peru, Benfer (1984) found no evidence of decreased dimorphism in stature with the advent of agriculture (8000–4500 BP), but he did observe diminished sexual dimorphism in bony response to musculature. Larsen (1984) found that sexual dimorphism increased with the adoption of maize agriculture in coastal Georgia (ca. 1115 AD), associated with a relative decline in female stature. He argues that this may be because women cultivated maize, while men remained hunters. Perzigian et al. (1984) also found that sexual dimorphism was greater among maize agriculturalists (ca. 700–1600 AD) than hunter-gatherers (before 1000 BC) in the Ohio River Valley. Cook (1984) found no changes in sexual dimorphism related to

changes in subsistence in the Lower Illinois River Valley. Goodman et al. (1984) found no significant changes in sexual dimorphism with the advent of maize agriculture at Dickson Mounds in Illinois (950–1300 AD).

Archaeological evidence has limitations for testing hypotheses about the causes of variation in sexual dimorphism. In many cases the hypothesis relating changes in sexual dimorphism to changes in subsistence in archaeological populations is post hoc. The alternative hypothesis that sexual dimorphism is related to polygynous mating may not be testable in archaeological populations, because marriage practices are not known. Many of the changes in sexual dimorphism with agriculture are inconsistent across populations. Other problems in the analysis of sexual dimorphism in archaeological populations include small samples of males and females from which to estimate sexual dimorphism, problems of sexing, and the difficulty of estimating stature from bones (Hamilton, 1982).

The sexual division of labor hypothesis can also be tested on ethnographic populations. Wolfe and Gray (1982b) tested whether contemporary agricultural populations are less sexually dimorphic than modern hunter-gatherers. They used a sample of 73 societies from the Standard Cross-Cultural Sample (Murdock and White, 1969) for which stature data for males and females were available. They found that agriculturalists were more sexually dimorphic than hunter-gatherers, contrary to the prediction of the hypothesis. Again, similarities among populations were not adequately controlled for in this study. We show below that hunting and agriculture, like sexual dimorphism, are highly significantly associated with phylogeny.

Two aspects of the sexual division of labor might affect sexual dimorphism in stature. First, the effect of different types of subsistence on sexual dimorphism was tested. Is there is a positive relationship between sexual dimorphism in stature and reliance on hunting, a primarily male activity? Is there is a negative relationship between sexual dimorphism in stature and agriculture, an activity that is shared more equally between the sexes? Second, the relative contribution to total food production by men

and women was calculated, and it was tested whether there is an association between sexual dimorphism in stature and the amount of work done by males and females in a population.

Nutrition

One possible cause of variation in sexual dimorphism that could not be directly investigated here is nutritional status. Information about nutritional intake was lacking for most of the populations in the sample. It has been hypothesized that well-nourished populations are more sexually dimorphic than malnourished populations, because male growth is more susceptible to nutritional deficiencies during development than female growth (Hiernaux, 1968; Hamilton, 1982). A different developmental reaction norm to variance in nutritional intake in males and females could reflect different fitness consequences of variation in height for males and females. Hamilton (1982) reviewed evidence that childbirth and lactation impose stabilizing selection on female size in nutritionally stressed populations.

Although nutritional status may be one of several causes that affect sexual dimorphism in stature, it is unlikely to explain all cross-cultural variation in sexual dimorphism. Eveleth (1975) found that across continents, African populations were the least dimorphic, but Native Americans were more dimorphic than Europeans, which is unlikely to be explicable in terms of better nutrition among Native Americans. Here, we will argue that the degree of sexual dimorphism may be determined by the relative nutritional status of boys and girls.

Secular change in stature

This study focuses on the long-term effects of the different traditional subsistence practices, and not on the consequences of recent urbanization and industrial development. Industrial populations have undergone a secular increase in stature in the past century (Eveleth and Tanner, 1990). This may increase sexual dimorphism, particularly in its early stages, because male growth is more sensitive to environmental conditions (Brauer, 1982). Populations from industrial-

ized countries (Europe and Japan) were not included in the sample.

A literature review of secular changes in stature in the populations in the sample indicates that a positive secular trend was not a general feature of the populations in the sample at the dates when the stature measurements were taken. This review covered only the years when the stature measurements in the sample were taken (mostly before 1970). A summary of patterns of secular change in populations in the sample, where known, follows: in Africa, no secular change in stature occurred in Bantu-speaking South Africans (ca. 1919–1973) (Tobias, 1989) or in rural populations in Mali, West Africa (including the Fulani and Mossi, 1917–1985) (Prazuck et al., 1988). Secular increase in stature has been observed in the Kalahari San (from ca. 1900–1962) (Tobias, 1962). In Asia, an overall secular decline in stature has been observed in India over the years 1881–1963 (populations including the Toda, who experienced an increase in stature, and the Oraons and Bhil, who experienced a decrease in stature) (Ganguly, 1979). A secular increase in stature was observed in males but not in females in the Tungus, otherwise known as the Evenki (from ca. 1900–1992) (Leonard et al., 1996). In America, a secular increase in stature was observed in the Western Apache (1940–1967) by Miller (1970), but other studies indicate stable or decreasing stature in Apache (1935–1961) and Navaho and Papago groups (early to mid-20th century) (Moore, 1972). No stature increase was observed in the Yucatec Maya (1895–1968) (McCullough, 1982). A secular increase in stature was observed in Australian Aborigines (1930–1970) (Barrett and Brown, 1971). Variable patterns of secular change were recorded in Papua New Guinea (ca. 1900–1981) (Ulijaszek, 1993). In Fiji, a secular trend was seen in the years 1970–1985, but not in the years 1930–1970 (Clegg, 1989).

Tobias (1985) surveyed evidence of a secular trend in subsistence-level populations in the 20th century. He found evidence for a positive secular trend in hunter-gatherers but not generally among agriculturalists. This pattern is also seen in the present sample (e.g., the !Kung and Australian Ab-

origines). Insofar as a secular increase in height also increases dimorphism (Brauer, 1982), the effect of the secular trend among hunter-gatherers would be to favor the hypothesis that sexual dimorphism is associated with hunting. No support was found for this hypothesis in the present analysis. It is concluded that secular changes in stature probably do not influence the results of this study.

We have ignored the question of whether cross-cultural variation in sexual dimorphism is a genetic trait, or an aspect of phenotypic plasticity. Rogers and Mukherjee (1992) argued that it is doubtful whether there has been sufficient time and stability in cultural behaviors for genetic variance in sexual dimorphism to evolve across populations. But the distinction between genetic and phenotypic traits does not greatly matter when investigating the adaptive value of a trait. Both phenotypic and genetic traits can be adaptive. Phenotypic plasticity is an adaptation which allows individuals to respond adaptively to their environment, in this case, during growth and development. The reaction norm of developmental response to the environment is heritable, although the resulting phenotype (e.g., stature) is a response to the environment.

METHODS

The dataset

Data on stature were taken from a variety of published sources (see Table 1). Only populations that included at least 20 individuals of each sex were included.

Further criteria for inclusion in the dataset were as follows. Firstly, all populations are found in the *Ethnographic Atlas* (Murdock, 1967, and in a revised spreadsheet version by Murdock, via personal communication from Patrick Gray). Stature samples were considered to come from cultures in the *Ethnographic Atlas* if they had the same name as a single culture (e.g., Zulu), or if they came from the same cultural "cluster" (a group of similar cultures sharing a common ancestor within the past 1,000 years) and had the same geographical location as a single culture within the cluster. In the latter case, the stature sample was assigned to the culture in that cluster with the same

TABLE 1. Populations in the sample listed by regions given in Murdock (1967)

Ethnic group ¹	E.A. code ²	Males		Females		Reference ⁵
		n ³	Ht ⁴	n	Ht ⁴	
A: Populations in sub-Saharan Africa						
Ashanti	Af3	48	164.2	27	154.7	Rattray, 1923
Bamileke	Ae5	352	168.4	236	158.6	Hiernaux, 1968
Bamum	Ae50	71	171.5	58	163.1	Hiernaux, 1968
Basa	Ah11	90	167.9	52	159.2	Hiernaux, 1968
Duala	Ae12	75	169.1	50	156.9	Hiernaux, 1968
Ganda	Ad7	61	163.6	66	156.2	Eveleth and Tanner, 1976
Ganda	Ad7	261	167.3	242	156	Hiernaux, 1968
Hadza	Aa9	36	160.5	31	150	Eveleth and Tanner, 1976
Ibo	Af10	68	165.5	54	154.5	Hiernaux, 1968
Kikuyu	Ad4	412	163.6	100	151.6	Orr and Gilks, 1931
Maasai	Aj2	362	165.9	333	152.4	Orr and Gilks, 1931
Maasai	Aj2	88	171.2	180	159.9	Sellen, 1995
Mbuti (Eastern, or Ituri Pygmies)	Aa5	71	144.4	38	136.0	Cavalli-Sforza, 1986, or Eveleth and Tanner, 1990
Mbuti	Aa5	510	144.0	382	137.0	Hiernaux, 1968
Mbuti	Aa5	69	144.2	32	137.4	Cavalli-Sforza, 1986
Mossi (Haute-Volta)	Ag47	49	167.8	58	158.6	Froment and Hiernaux, 1984
	Ag47	27	168.9	119	158.7	Froment and Hiernaux, 1984
Nama	Aa3	73	162.4	27	149.7	Shapira, 1930
San ("Bushmen")	Aa1 (!Kung) ⁶	292	159.4	346	150.0	Eveleth and Tanner, 1976
San	Aa1	58	157.7	77	146.6	Hiernaux, 1968
San	Aa1	22	159.3	22	148.8	Shapira, 1930
Turkana	Aj5	40	173.9	42	163.3	Sellen, 1995
Venda	Ab6	168	167.6	56	154.0	Hiernaux, 1968
Yoruba	Af6	340	167.5	205	155.0	Eveleth and Tanner, 1976
Zulu	Ab12	106	166.1	219	156.0	Eveleth and Tanner, 1976
B: Populations in the Circum-Mediterranean						
Algerians	Cd12	96	172.5	29	160.8	Eveleth and Tanner, 1976
Druze (Near East)	Cj8	181	165.6	114	152.2	Shanklin and Izzeddin, 1937
Egyptians	Cd2		171.6		159.2	Eveleth and Tanner, 1990
Fulani, or Peul (Niger)	Cb8 (Bororo) ⁷	42	172.7	41	161.7	Hiernaux, 1968
Fulani	Cb8	32	176.3	30	164.6	Sellen, 1995
Kurds (Iraq)	Ci11	598	166.1	31	152.7	Field, 1952
Nubians (mainly Kenuzi and Fedichi)	Cd1 (Kenuzi Nubians)	127	169.5	282	157.4	Valsik et al., 1970
C: Populations in Asia						
Bhil (India)	Ef5	56	158.8	46	149.5	Field, 1970 (pp. 4 and 176)
Chukchi (Siberia)	Ec3	70	165.1	82	152.6	Smirnova, 1979
Khalka Mongols	Eb3	59	164.8	49	151.3	Eveleth and Tanner, 1976
Khasi (India)	Ei8	100	156.7	65	147.0	Field, 1970 (pp. 201–203)
Koreans	Ed1	280	170.1	49	156.2	Eveleth and Tanner, 1976
Muria Gond (India)	Eg13	52	157.8	52	147.9	Field, 1970 (pp. 3 and 176)
Oraons (India)	Ef6	100	160.4	110	149.4	Field, 1970 (pp. 6 and 176)
Punjabis	Ea13 (West Pun- jabis)		168.3		155.8	Eveleth and Tanner, 1976
Toda (India)	Eg4	25	170.3	25	153.0	Field, 1970 (pp. 21–22 and 176–177)
Toda	Eg4	61	168.3	58	153.7	Field, 1970
Toda	Eg4	82	169.8	25	155.6	Field, 1970
Toda	Eg4	73	171.9	39	157.7	Field, 1970
Tungus	Ec9 (Goldi ⁸)	52	156.5	72	146.5	Skeller, 1954
Wood Nenetz (Siberia)	Ec4 (Yurak ⁹)	50	160.1	42	147.6	Smirnova, 1979
D: Populations in the Southeast Asia, the Pacific Islands, and Australia						
Southeast Asia						
Ami (Taiwan)	Ia9	146	164.6	94	155.9	Chai, 1967
Atayal (Taiwan)	Ia1	96	160.1	147	149.8	Chai, 1967
Banun (Taiwan)	Ia10	96	157.2	110	146.2	Chai, 1967
Paiwan (Taiwan)	Ia6	127	156.6	150	148.0	Chai, 1967
Javanese	Ib2		158.0		150.0	Eveleth and Tanner, 1976
Manus	Ig9	20	162.9	20	151.0	Eveleth and Tanner, 1976
Pacific Islands						
Lau (Solomon Islands)	Ih4	20	164	38	153.4	Eveleth and Tanner, 1990
Ontong Java	Ii5	75	166.2	119	156.0	Eveleth and Tanner, 1990
Kwaio	Ie13	46	161.0	49	149.7	Eveleth and Tanner, 1990
Western Samoa	Ii14	101	170.4	144	158.3	Eveleth and Tanner, 1990
American Samoa	Ii1	43	172.8	88	162.7	Eveleth and Tanner, 1990
American Samoa	Ii1	425	170.8	610	160.3	Eveleth and Tanner, 1990

TABLE 1. (continued)

Ethnic group ¹	E.A. code ²	Males		Females		Reference ⁵
		n ³	Ht ⁴	n	Ht	
Australia						
Australian Aborigines (mostly Wal-	Id10 (Walbiri)	39	172.1	23	162.9	Eveleth and Tanner, 1990
biri)						
Papua New Guinea						
Kiwai	Ie13	25	168.3	25	157.3	Hyndman et al., 1989
	<i>E: Populations in North America</i>					
Angmagsalik Inuit	Na24	166	162.0	203	153.3	Skeller, 1954
Apache	Nh11 (Western	31	168.4	46	153.3	Eveleth and Tanner, 1976
	Apache)					
Blackfeet	Ne12	38	177.4	46	164.8	Eveleth and Tanner, 1976
Chippewyan	Na30	44	166.4	20	150.9	Skeller, 1954
Copper Inuit	Na3	82	164.8	42	156.4	Jenness, 1923
Greenland Inuit	Na25	500	162	400	152	Skeller, 1954
Iglulik Inuit	Na22	20	166	20	153.7	Jenness, 1923
Labrador Inuit	Na23	58	158.4	78	148.3	Skeller, 1954
Navaho	Nh3	90	169.6	33	154.2	Hrdlicka, 1935
Nootka	Nb11	33	168.7	42	158.2	Birkbeck and Lee, 1973
Papago	Ni2	50	170.9	30	155.9	Comas, 1971, or Hrdlicka, 1935
Pima	Ni6	53	171.8	30	157.4	Comas, 1971, or Hrdlicka, 1935
Pima	Ni6	77	169.6	51	156.3	
Tarahumara	Ni1	50	163	30	150.8	Comas, 1971
Tarasco	Nj8	50	163.1	30	150.8	Comas, 1971
Tarasco	Nj8	111	161.8	157	151.2	Comas, 1971
Totonac ¹⁰	Nj4	100	158.0	100	146.3	Comas, 1971
Zuni	Nh4	60	163.5	32	151.2	Hrdlicka, 1935
	<i>F: Populations in South America</i>					
Alacaluf	Sg5	28	156.4	34	146.3	Steggarda, 1963
Aymara	Sf2	66	164.1	66	151.4	Eveleth and Tanner, 1990
Aymara	Sf2	45	160.0	69	149.6	Eveleth and Tanner, 1990
Aymara	Sf2	70	163.0	90	150.0	Eveleth and Tanner, 1990
Aymara	Sf2	62	159.9	58	148.1	Eveleth and Tanner, 1990
Aymara	Sf2	57	163.1	60	149.8	Eveleth and Tanner, 1990
Aymara	Sf2	25	162.0	39	149.0	Eveleth and Tanner, 1990
Barama River	Sc3	104	156.8	99	145.8	Steggarda, 1963, or Gillen, 1936
Caribs						
Cayapo	Sj9	110	165.4	156	153.9	Eveleth and Tanner, 1976
Macusi	Sc12	42	156.8	28	146.3	Steggarda, 1963
Mataco	Sh1	30	163.8	20	152.9	Steggarda, 1963
Maya	Sa6	77	155.1	56	142.7	Comas, 1971
Maya	Sa6	128	155.4	94	141.8	Comas, 1971
Maya	Sa6	42	156.8	20	142.8	Eveleth and Tanner, 1976
Miskito	Sa9	30	164.0	32	154.0	Eveleth and Tanner, 1990
Quiche	Sa13	117	153.8	83	143.8	Comas, 1971
Toba	Sh8	190	167.8	212	157.7	Comas, 1971
Xavante	Sj11	42	170.2	39	156.3	Comas, 1971, or Eveleth and Tanner, 1976
Yanomama	Sd9	316	153.2	260	142.3	Eveleth and Tanner, 1976

¹ Name of ethnic group (and region or country where this may be ambiguous).² Code given to this culture in the *Ethnographic Atlas* (Murdock, 1967).³ Sample size (n).⁴ Mean height cm.⁵ Published reference of data on height.⁶ Unclear from stature sources which group of San were studied. The !Kung are the largest population in Murdock's "Bushman" (i.e., San) cluster. The Naron (an alternative possibility) are also hunter-gatherers with similar sexual division of labor and marriage practices.⁷ Located on the border of Niger and Nigeria.⁸ Goldi is the only culture in the Tungus cluster of Murdock (1967). Tungus are known today as Evenki.⁹ Yurak is an ethnonym of Nenets.¹⁰ The Totonac were excluded from the final analysis because the *Ethnographic Atlas* has no information on their marriage practices.

geographical location. Any ambiguities in assigning stature samples to cultures in the *Ethnographic Atlas* are noted in Table 1. All cultures included in the dataset also had information about their means of subsistence, marriage practices, and sexual division of labor in the *Ethnographic Atlas*.

All populations in the sample are also included in the *History and Geography of Human Genes* (Cavalli-Sforza et al., 1994, Appendix 3), which includes information about the genetic relationships of hundreds of different populations worldwide. All populations included are "aboriginal," defined as populations which inhabited their present location before 1492 (Cavalli-Sforza et al., 1994). Thus all American populations included in the current dataset are Native Americans, using the term to include Inuit (Eskimos) and South American Indians. As previously stated, populations from Europe and Japan were not included.

The criteria for inclusion outlined above resulted in a dataset of 76 populations, which are shown in Table 1A–F. Populations are listed by region, following Murdock (1967). Table 1 also lists the *Ethnographic Atlas* reference code for each population, the mean stature of males and females in that population, and the source of the stature data for each population. The geographical location (latitude and longitude) of each population was also taken from the *Ethnographic Atlas*.

Type of subsistence. The *Ethnographic Atlas* (Murdock, 1967) includes information about five types of subsistence activity: hunting, gathering, fishing, pastoralism, and agriculture. The percentage which each subsistence activity contributes to total food production in each culture is coded in column 7 of the *Ethnographic Atlas*. The amount of hunting and agriculture (as a percentage of total food production) in each population was taken from this source.

The sexual division of labor. The sexual division of labor for each type of subsistence activity is also coded (columns 54–62). Codes of male and female contribution to food production in the *Ethnographic Atlas* were recoded for use in this analysis, as shown in

TABLE 2. Adaptation of *Ethnographic Atlas* (E.A.) codes on sexual division of labor (Murdock, 1967, columns 54–62)

E.A. code	Estimated % contribution by women
M	0
N	25
D	50
E	50
G	75
F	100
P	Missing value

Table 2. To estimate the overall sexual division of labor in each society, the percentage contributed by women to each type of subsistence activity was multiplied by the percentage contributed by that type of subsistence activity to total food production in each population. The total percentage of work done by women in each population was calculated by summing the contribution of women to each of the five types of subsistence activity.

Marriage. The *Ethnographic Atlas* classifies marriage as polyandrous, monogamous, "occasionally polygynous" (i.e., "polygyny is occasional or limited"), or "generally polygynous" (i.e., "polygyny is common or general") (Murdock, 1967, column 14). From this information, an ordinal scale of frequency of polygyny can be formed. There were no polyandrous cultures in the sample. Monogamous populations were given a score of 1. Populations which practice occasional polygyny were given a score of 2. Populations where polygyny is common or general were given a score of 3. This ordinal scale was intended to measure the amount of competition for females experienced by males, which was assumed to be closely related to marriage norms in any particular society. Marriage can also be scored as a two-state discrete character, either as "generally polygynous" vs. all other states, or "any polygyny" vs. no polygyny. The comparative analysis carried out (below) was performed both with marriage as a discrete variable and an ordinal variable, and it made no difference to the results.

Statistical analysis

Measuring sexual dimorphism. Variation in sexual dimorphism among popula-

TABLE 3. *Horizontal and vertical transmission of traits among populations*¹

Dependent variable	Phylogenetic relative(s)			Geographical neighbor(s)		
	Slope	SE of slope	Significance of slope	Slope	SE of slope	Significance of slope
Sexual dimorphism	0.41	0.13	0.002	0.27	0.15	0.07
Women's work	0.24	0.13	0.07	0.50	0.15	0.002
Hunting	0.45	0.17	0.008	0.12	0.15	n.s.
Agriculture	0.33	0.13	0.01	0.33	0.15	0.03
Polygyny	0.42	0.15	0.005	0.14	0.15	n.s.

¹ Multiple regression results, showing the association of each trait with phylogeny (phylogenetic relatives) and geographical proximity to other populations (nearest neighbors). The significance values shown are of partial regression coefficients. All multiple regressions were highly significant overall (F significant at 0.0002 or less).

tions was measured using residuals from the reduced major axis. This differs from previous studies, which measured sexual dimorphism using a ratio of male to female stature (e.g., Alexander et al., 1979; Gray and Wolfe, 1980; Gaulin and Boster, 1992). However, for allometric traits (such as dimorphism in stature), the size of ratios is not independent of body size. For sexual dimorphism in humans, the ratio of male height to female height increases with body size (Gaulin and Boster, 1985; Ranta et al., 1994). Using residuals controls for the effect of body size, in order to discover which populations are less or more sexually dimorphic than expected for a given body size. The line fitted is the reduced major axis, or Type II model, because both male and female stature estimates have a degree of associated error (Harvey and Mace, 1982). The relationship between female and male stature is shown in Figure 3.

Horizontal and vertical transmission of biocultural traits. In our investigation into the transmission of traits among populations, phylogenetic relatives were defined as the sister-group of each population on a genetic tree (Fig. 1, described below). Most populations could be compared to a single other population, with which they formed a paired clade at the tips of the tree (e.g., the Kikuyu and Ganda). In cases where there or more daughter populations descended from a single node (e.g., the Pima, Papago, and Zuni), each population was compared to all other populations in the clade. The mean value of each trait in the other populations in the clade was used. In some cases (e.g., the Mbuti), a population was coordinate with a larger clade. In these cases the popu-

lation was compared to all populations in the coordinate clade. Again, the mean value of each trait for all the other populations in the coordinate clade was used.

Nearest geographical neighbors were found using great-circle distances. Each population was compared to the same number of phylogenetic relatives and geographical neighbors. Thus, populations which were compared to a single phylogenetic relative were also compared to a single geographical neighbor (the nearest population). Populations compared to two or more phylogenetic relatives were compared to an equal number of their nearest geographical neighbors. Where populations were compared to more than one geographical neighbor, the mean of the value of each trait in all geographical neighbors was used.

Multiple regression was used to investigate the association between each trait in the populations in the sample (the dependent variable) and in their phylogenetic relatives and geographical neighbors (the independent variables). Five multiple regressions were performed, one for each variable whose transmission was tested. These included: degree of sexual dimorphism (residuals of the reduced major axis of male stature and female stature), women's work as a percentage of total subsistence, hunting, agriculture, and amount of polygyny. The multiple regression results are shown in Table 3.

Phylogenetic comparative analysis. Felsenstein's method of comparative analysis using independent contrasts, designed to control for similarity by descent among populations, was used to test for evolutionary correlates of cross-cultural variation in

sexual dimorphism in stature (Felsenstein, 1985; Pagel, 1992). In this method, all populations are placed on a phylogeny, or a tree showing the ancestral relationships among those populations. Independent contrasts are differences in character states among daughter populations descended from a single node, or between nodes descended from a higher node. Statistical analysis is carried out on independent contrasts, testing for correlated evolutionary change among variables.

Two different trees were used to estimate phylogeny, or ancestral relationships among populations. This was to ensure that any effects found were not an artifact of a particular tree. The first is a genetic tree adapted from Cavalli-Sforza et al. (1994), shown in Figure 1. It is a composite tree based on the F_{ST} genetic distance trees of Cavalli-Sforza et al. (1994). Higher nodes follow their world tree (Fig. 2.3.2.B, in Cavalli-Sforza et al., 1994). Lower nodes follow their genetic trees for individual continents or subcontinental regions. Where there were conflicts among the source trees in Cavalli-Sforza et al. (1994), the tree in which populations were distinguished at a lower level was used. Seventy independent contrasts were generated from the genetic tree.

A second tree was a language tree. The language tree used here follows Ruhlen (1991), assuming a monophyletic origin of languages. Fifty-one independent contrasts were generated from the language tree. This is lower than the number of contrasts from the genetic tree, because the language tree is less resolved, especially among higher nodes. The language tree is shown in Figure 2.

Independent contrasts were generated after the method of Pagel (1992), implemented by the computer program CAIC (comparative analysis by independent contrasts) (Purvis and Rambaut, 1995). Correlated evolutionary change in sexual dimorphism and the cultural and economic variables hypothesized to be associated with it (polygyny, hunting, agriculture, and women's work) were investigated by multiple regression, using SPSS (Norušis, 1994). The dependent variable was independent contrasts in sexual dimorphism (residuals of the reduced major

axis of male stature and female stature). The independent variables were independent contrasts in women's work, polygyny, agriculture, and hunting. The regression is through the origin, because independent contrasts are a measure of differences among sister populations, not actual character values (Pagel, 1992). Unresolved nodes were resolved on women's work, as the main independent variable.

RESULTS

Sexual dimorphism in the sample

Mean male stature in the sample ranged from 144 cm in the Mbuti to 177 cm in the Blackfeet. Mean female stature ranged from 137 cm in the Mbuti to 165 cm in the Blackfeet. Male stature ranged from 4–10% larger than female stature. The relationship between male and female height, fitting the reduced major axis is:

$$\text{Male height} = 1.09 (\text{female height}) - 3.24 \text{ cm.}$$

This level of variation in sexual dimorphism in stature is comparable to that found in previous studies. The coefficient of determination (r^2) of the reduced major axis of male stature on female stature was 0.89, i.e., 89% of the variance in male stature is "explained" by the variance in female stature, leaving 11% of the variance in male stature to be accounted for by other factors. The regional distribution of this variation showed similar regional variation to that found by Eveleth (1975). Africans were the least dimorphic populations, Asians showed intermediate dimorphism, and Native Americans were the most dimorphic populations. The relationship between male and female stature is shown in Figure 3.

Horizontal and vertical transmission of biocultural traits

Four out of five traits showed a highly significant association with phylogeny (phylogenetic relatives), including degree of sexual dimorphism, hunting, agriculture, and polygyny. Women's work had a marginally significant association with phylogeny. Two traits also showed an association with geographical neighbors, i.e., women's work

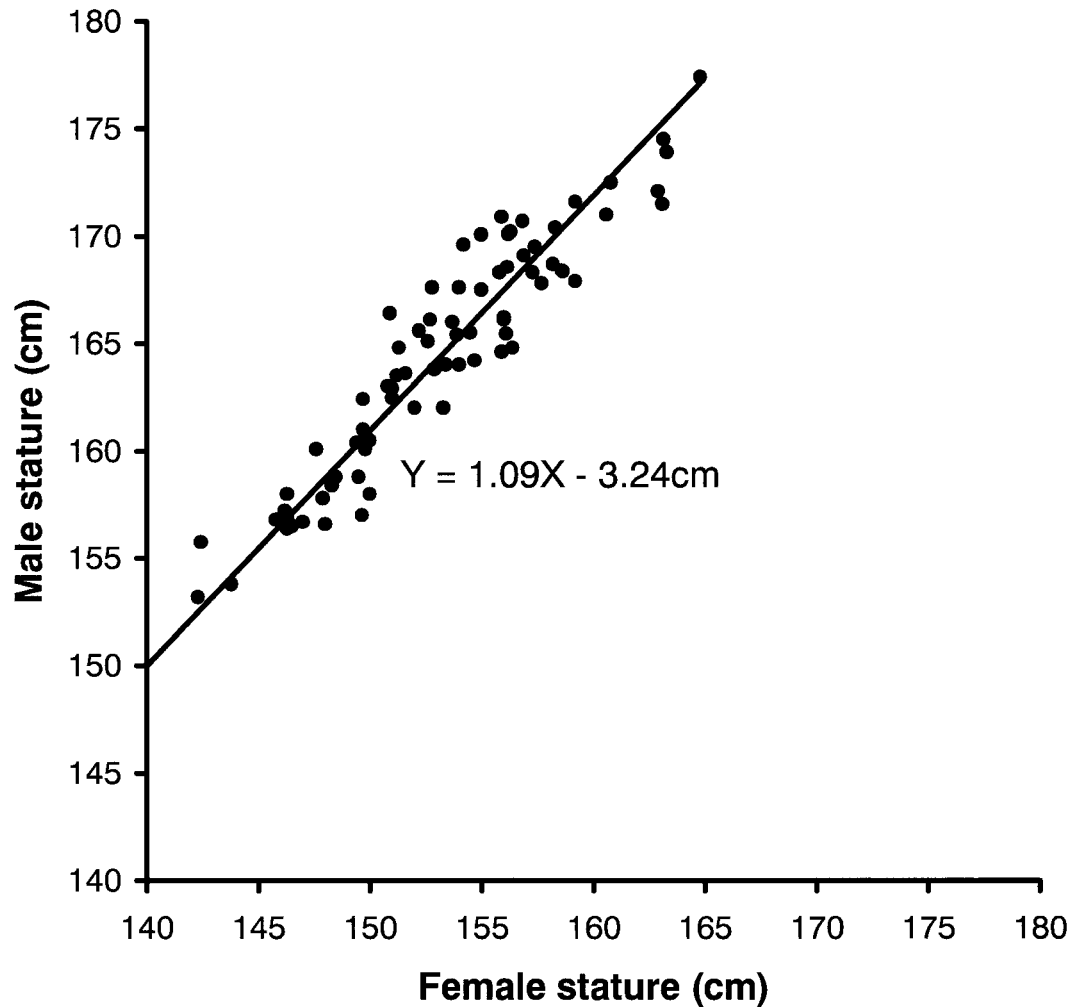


Fig. 3. Male and female stature in the sample. The line fitted is the reduced major axis. Residuals of the reduced major axis were used to measure cross-cultural variance in sexual dimorphism.

and agriculture. The degree of sexual dimorphism had a marginally significant association with geographical neighbors. These results are shown in Table 3.

Phylogenetic comparative analysis

Independent contrasts in sexual dimorphism (residuals of the reduced major axis of male stature on female stature) are negatively associated with women's work (as a percentage of total subsistence labor). There was no relationship between independent contrasts in sexual dimorphism and po-

lygyny, or between sexual dimorphism and either hunting or agriculture. These results are shown in Table 4.

Both male and female stature appear to be affected by the proportion of work done by women, although they are affected in different directions. This was shown by performing two additional multiple regressions, testing the effect of independent contrasts in women's work on male and female stature separately. Contrasts in mean stature in the two sexes are highly significantly associated. In addition, contrasts in male stature

TABLE 4. *Sexual dimorphism and women's work*¹

Tree	Overall regression model			Independent variable: women's work		
	Multiple R	Adjusted R ²	F	Slope	SE slope	Significance
Genetic tree	0.28	0.08	6.07	-0.031	0.013	0.02
Language tree	0.40	0.16	9.65	-0.042	0.013	0.003

¹Variables not in the equation: hunting, agriculture, and polygyny. Multiple regression results of independent contrasts from the genetic and language tree. The dependent variable is independent contrasts in sexual dimorphism (residuals of the reduced major axis of male and female stature). Independent variables are independent contrasts in amount of women's work, hunting, agriculture, and polygyny.

TABLE 5. *Independent contrasts in stature*

A. Relationship between men's stature and independent variables ¹							
Tree	Women's stature			Women's work (%)			
	Slope	SE slope	Significance	Slope	SE slope	Significance	
Genetic tree	1.041	.045	<0.0001	-0.029	0.013	0.02	
Language tree	1.057	0.053	<0.0001	-0.041	0.014	0.004	

B. Relationship between women's stature and independent variables ²							
Tree	Men's stature			Women's work (%)			
	Slope	SE slope	Significance	Slope	SE slope	Significance	
Genetic tree	0.85	0.037	<0.0001	0.029	0.011	0.01	
Language tree	0.84	0.042	<0.0001	0.036	0.012	0.005	

¹Multiple regression against independent contrasts in female stature and women's work. Significance of overall multiple regression <0.0001.

²Multiple regression against independent contrasts in male stature and women's work. Significance of overall multiple regression <0.0001.

are negatively associated with contrasts in women's work, while contrasts in female stature are positively associated with contrasts in women's work. These results are shown in Table 5A,B.

DISCUSSION AND CONCLUSIONS

Horizontal and vertical transmission of biocultural traits

Four out of the five traits tested showed a highly significant association with phylogeny. These included degree of sexual dimorphism, hunting, agriculture, and marriage. The other trait tested, women's work, was also marginally associated with phylogeny. This indicates that these traits are inherited phylogenetically, from mother to daughter populations. This implies that it is essential to control for similarity by descent when investigating correlations among characters, or between a character and an environmental variable, in cross-cultural comparison in humans.

Three out of the five variables (women's work, variation in sexual dimorphism, and agriculture) also showed an association with geographical proximity. This indicates that

these traits are transmitted between neighboring populations (horizontally), and/or are adaptations to different geographical environments. In the phylogenetic model used here, horizontal transmission is statistically equivalent to independent evolution of a trait. If a trait is consistently adopted in association with another trait or environmental variable, it is evidence of correlated evolution between the two.

Phylogenetic comparative analysis

The sexual division of labor: Sexual dimorphism in stature is negatively correlated with women's work. This is consistent with the hypothesis that cross-cultural variation in sexual dimorphism in stature is related to variation in male and female foraging strategies, especially the overall sexual division of labor. However, no specific association between hunting or agriculture and sexual dimorphism was found (see below; cf. Frayer, 1980, 1981; Brace and Ryan, 1980).

The negative association between women's work and dimorphism may result from cross-cultural variation in sex-biased parental investment, affecting childhood nutri-

tion, associated with variation in the overall sexual division of labor. Parental investment theory predicts that parents should invest more in offspring of one sex when that investment increases the parent's own inclusive fitness (Clutton-Brock, 1991). Children who act as "helpers at the nest," who are engaged in food production which benefits their parents or siblings, may receive more parental investment. Where males perform all or most subsistence labor, it may be adaptive for parents to invest more resources in their sons than daughters, insofar as the returns to parents (in terms of food production by children) are greater for sons than daughters. As a result, males would achieve a greater proportion of their potential adult stature than females. Sexual dimorphism would increase as a consequence. Conversely, in societies where females perform a large proportion of subsistence labor, parents may invest relatively more in their daughters, so that girls' growth is not compromised relative to boys' growth. Sexual dimorphism would therefore be diminished.

The greater value of male children in household production is often cited both by researchers and parents as a reason for male-biased parental investment (Arnold and Zhaoxiang, 1987; Bairagi, 1986; Levine, 1987; Smith and Smith, 1994; however, cf. Das Gupta, 1987 for an opposing view). Sex biases in parental investment are known to affect children's nutritional status, which in turn affects adult stature. There is good evidence from some South Asian populations that parental discrimination against girls can involve feeding them less both in quantity and quality of food (Bairagi, 1986; Chen et al., 1981; Levine, 1987; Das Gupta, 1987). This results in greater levels of malnutrition (affecting growth) among girls, as well as higher female child mortality rates (Chen et al., 1981; Bairagi, 1986). However, discrimination against girls is not a universal pattern. In some parts of Africa, for example, girls are consistently found to be better nourished than boys (Quinn et al., 1995; Madise and Mpoma, 1997). It is suggested here that these variations in sex-bias in parental investment may be related to the greater contribution of females to subsis-

TABLE 6. *Women's work as a percentage of total subsistence work by region*

Region	Number of cultures	Mean % women's work	SD % women's work
Africa	18	51.1	12.58
Circum-Mediterranean	6	21.7	5.9
Asia	11	27.3	18.42
Island Pacific	13	43.5	11.55
North America	16	18.6	15.59
South America	12	33.5	15.38

tence in sub-Saharan Africa compared to Asia and Native America.

In the sample used in the present analysis, women's work varies between regions. To illustrate this, populations were divided by region, following the six geographical regions of the world of Murdock (1967) (e.g., Table 1). The "Circum-Mediterranean" includes North Africa and the Middle East. The mean and standard deviation in women's work (as a percentage of total subsistence) in each region are shown in Table 6. Analysis of variance showed a highly significant difference in women's work between regions ($F = 11.53$, $p < 0.0001$). A post hoc Bonferroni test found a significant difference ($p < 0.05$) between Africa and all other continents except the Island Pacific, and between the Island Pacific and the Circum-Mediterranean. This variance in women's work between regions is consistent with regional variation in sexual dimorphism, which is least in sub-Saharan Africa and highest in Native Americans. This pattern is consistent with the suggestion that sexual dimorphism is influenced by the sexual division of labor, perhaps because the sexual division of labor affects the amount of food received by boys and girls during development.

Sex-biased juvenile mortality shows the same geographical patterns as variance in sexual dimorphism. Male juvenile mortality is "normally" expected to be higher than female juvenile mortality, because males are biologically more vulnerable than females. However, higher female than male child mortality is observed in regions where women contribute relatively little to subsistence, including South and East Asia (Das Gupta, 1987; Bairagi, 1986; Arnold and Zhaoxiang, 1986), and historically in the North

American Inuit (Smith and Smith, 1994). In a cross-cultural study, Hewlett (1991) found that female-biased juvenile mortality was strongly statistically associated with a high male contribution to subsistence, as a consequence of male-biased parental investment in these societies. In sub-Saharan Africa, where women contribute more to food production, higher than expected male juvenile mortality is observed in some populations (Cronk, 1989; Harpending and Pennington, 1991).

Type of subsistence activity: hunting and agriculture. The type of subsistence activity, i.e., the amount of hunting or agriculture, showed no association with sexual dimorphism in stature. Sexual dimorphism in stature appears to be related to the overall sexual division of labor, but not to the kind of work (hunting or agriculture) done. The absence of any association between hunting and sexual dimorphism found here can be compared to the hypothesis of Frayer (1980) and Brace and Ryan (1980) that the large sexual dimorphism of the Late Pleistocene was associated with the large-game hunting economy. Modern hunter-gatherers inhabit more marginal habitats than Late Pleistocene hunters. Many modern hunter-gatherers, e.g., the !Kung San and the Walbiri, pursue a broad foraging economy where gathering is more important than hunting. Among these types of foraging economy, there may be no selection for large body size in male hunters. For example, Hill and Hurtado (1996) found that males with medium body size were the best hunters in the Ache, modern South American hunter-gatherers. However, the sample used here also includes Inuit populations, in which large-game hunting was a primary subsistence activity. It is concluded that in contemporary humans, neither hunting nor agriculture has any effect on sexual dimorphism. It is the amount of subsistence work done by men and women, rather than the type of subsistence practiced, which has an effect on sexual dimorphism in different societies.

Polygyny. There was no support for the hypothesis that variation in sexual dimorphism in stature is associated with po-

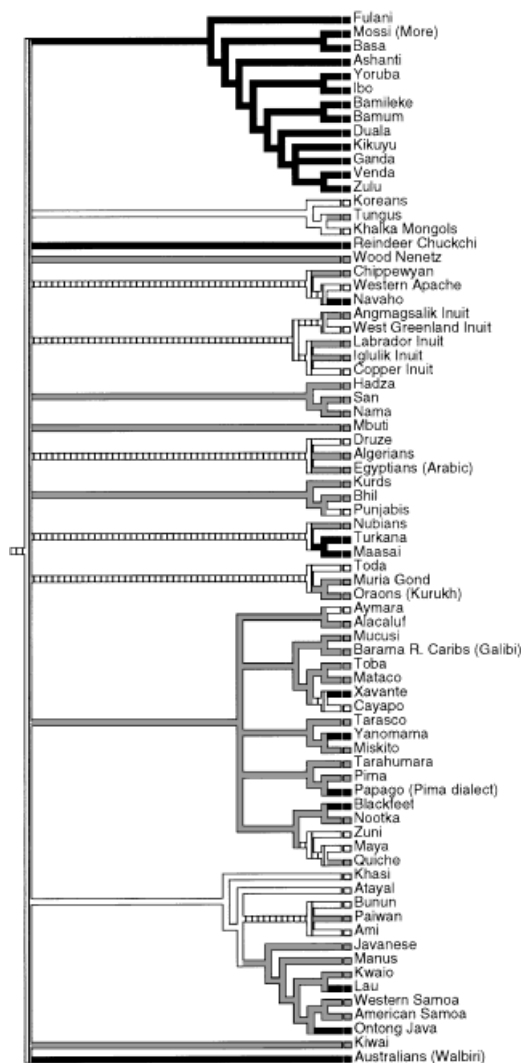


Fig. 4. Marriage practices in populations, mapped onto the language tree using parsimony (using MacClade, Maddison and Maddison, 1992). Black, general polygyny; grey, occasional polygyny; white, no polygyny. Hatched lines indicate ambiguous ancestral states.

lygyny. But there are several reasons to suspect that this might be a Type II error (failure to detect a real effect). Placing marriage practices on a phylogeny reveals that "general polygyny" is a highly clustered trait, mainly confined to the Niger-Kordofanian-speaking African clade (Fig. 4). The number of independent contrasts in this trait is small, increasing the likelihood of not detecting a real association in the data. This does

not mean that the method of comparative analysis of Felsenstein (1985) by independent contrasts lacks statistical power. Rather, this method reveals the real lack of independent cases on which this hypothesis can be tested.

It is also difficult to obtain accurate data on paternity and variance in male reproductive success, which may be only roughly correlated with marriage practices. Available data on marriage practices are also not ideal. The marriage codes of Murdock (1967) are rather crude categories, classifying all cultures in the sample into only three groups (no polygyny, low polygyny, and general polygyny). A quantitative estimate of the proportion of polygynous marriages in each population would be preferable. This would also increase the number of independent contrasts, increasing the probability of detecting any association between marriage practices and degree of sexual dimorphism.

However, from the available comparative data, it is concluded that cross-cultural variance in dimorphism is not associated with variation in marriage practices or sexual selection. In this respect, cross-cultural variation in humans differs from variation in sexual size dimorphism across other primate species, which appears to be sexually selected (Alexander et al., 1979; Leutenegger, 1982).

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